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ORIGINAL ARTICLE

Two new species of *Gondwanaspis* (Trilobita, Odontopleurida) from the Givetian-Frasnian transition of the northern Rhenish Massif (Germany)

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Abstract

The cosmopolitan genus *Gondwanaspis* is one of two post-Taghanic (late Givetian to Frasnian) odontopleurid genera and the only genus of the Odontopleurida surviving the Lower Kellwasser Event, finally disappearing at the Upper Kellwasser Event. Although it is known from the Frasnian of Australia, Germany, France, Morocco, and Russia, findings of the genus are comparatively rare. Here we present *Gondwanaspis eisbornensis* n. sp. from the probable lower Frasnian of the Beul section near Eisborn (northern Sauerland) and *Gondwanaspis schloesseri* n. sp. from possibly top-Givetian strata of the Hofermühle South Quarry of the Bergisches Land (Velbert Anticline), both in the northern Rhenish Massif. *Gondwanaspis schloesseri* n. sp. represents one of the few species of which both the cephalon and pygidium are known, while the holotype of *G. eisbornensis* n. sp. is one of the largest known specimens within the genus.

Keywords Devonian · Trilobites · Odontopleurida · Rhenish Massif · Biostratigraphy

Introduction

Trilobites are one of the major groups in Palaeozoic benthic communities. The Devonian is of special importance in their evolution due to the sequence of global extinction events, especially in the top-Eifelian to Famennian interval. Unlike most other trilobite groups, the odontopleurids did not flourish after their main spread during the Silurian. In the Early and Middle Devonian, they are represented by only a few genera and species (Basse and

Müller 2004; Feist and McNamara 2007). Most of these disappeared in the course of the global Taghanic Crisis at the middle/upper Givetian boundary (see Aboussalam 2003). Only two genera of the Odontpleuridae survived the crisis: *Koneprusia* Prantl and Přibyl, 1949 (e.g. Aboussalam 2003; Feist and McNamara 2007), representing the Koneprusiinae, and *Gondwanaspis* Feist, 2002, a member of the Acidaspidinae. The previously oldest known species of the second genus is *G. tenella* (Maximova, 1960) from the lower Frasnian *Ancyrodella rotundiloba* Zone (MN = Montagne Noire Zone 2 sensu Klapper 1989) of the Gryaznukha Brook outcrop, Rudny Altai, southern Siberia. A slightly younger early Frasnian species, *G. prisca*, was described by Feist and McNamara (2007) from the *Palmatolepis transitans* Zone (MN Zone 4) of the Montagne Noire, southern France. While *Koneprusia* went extinct at the Lower Kellwasser Event, *Gondwanaspis* persisted until the base of the Upper Kellwasser Event in three regions (Feist and McNamara 2007; Lerosey-Aubril and Feist 2012; McNamara and Feist 2016). No post-Kellwasser species of the Odontopleurida are known. Here we present new rare findings of *Gondwanaspis* from two localities of the northern Rhenish Massif, from the assumed top-Givetian and from the probable lower Frasnian. This extends the

stratigraphic range of the genus probably for the first time into the terminal Middle Devonian.

Localities

Beul near Eisborn

The outcrop is situated in a forest less than a km NW of Eisborn (Fig. 1). Coordinates are: 51°23'22,40"N - 7° 52'14,57'E (or x = ³⁴21.470, y = ⁵⁶95.590) on topographic sheet (1: 25 000) 4613 Balve. The small natural cliff documents the final depositional history of the famous, very thick Hönne Valley Reef Complex. Following the unpublished B.Sc. Thesis of Nowak (2010), a preliminary section description was given by Becker et al. (2016). A full survey of microfacies, macrofaunas, and conodont stratigraphy is provided by Stichling et al. (in press, this issue). The odontopleurid specimen was collected from a loose slab of reddish, thin-bedded limestone at the steep slope at the southwestern end of the cliff. Apart from the trilobite, the slab yielded brachiopods and reef builders, which characterise the Eisborn Member of the Hagen-Balve Formation. In the lower part of the slab, middle-grey bioclastic wackestones with a few thamnoporid branches are sandwiched between thin stromatoporids sheets, which give a coverstone fabric. Parts of the slab were treated as conodont sample, which yielded two specimens of *Polygnathus alatus*, some ramiform elements, and a fragmentary scolecodont. In the detailed section log of Stichling et al. (in press, this issue) beds with monotypic *Po. alatus* assemblages occur at the base of the section but re-appear in the middle part, above the entry of *Ancyrodella rotundiloba pristina*, the index taxon of the basal Frasnian *Ad. rotundiloba pristina* Zone (= MN Zone 1). Aboussalam and Becker (2007) showed that *Po. alatus* may enter in the top-Givetian *Skeletognathus norrisi* Zone. With respect to the unclear position within the section, we cannot be sure whether the odontopleurid comes from the top-Givetian or basal Frasnian part. However, the top-Givetian section base is thick-, not thin-bedded, and the position of the loose slab on the slope suggests derivation from higher, lower Frasnian parts.

Feist and Schindler (1994) described some trilobites of the genera *Cryphops* Richter and Richter, 1926, *Lioharpes* Whittington, 1950, and *Palpebralia* Richter and Richter, 1927 from the upper part of the succession, the middle/upper Frasnian Beul Formation, from below a dark Kellwasser limestone. Basse and Lemke (1996) and Basse (1996) mentioned a pygidium of *Scutellum* sp. C from the Frasnian without any further stratigraphic information. This specimen was later assigned to cf. *Frasniellum chingachgook* Basse and Müller, 2004.

Hofermühle south quarry

The quarry lies on the northern flank of the Velbert Anticline in the northwestern Rhenish Massif and is a protected natural site (Fig. 1). The outcrop consists of reefal (biostromal) limestones, which are interrupted by several marker black shales and coral marls. The odontopleurid specimens were collected in loose material on a steep slope in the older, southwestern part of the quarry. Coordinates are 51°18'10.80"N, 6°57'0.15"E (or x = ²⁵66.299, y = ⁵⁶85.785) on topographic sheet (1: 25 000) 4607 Kettwig. The abandoned Hofermühle South Quarry is a famous fossil site for rugose and tabulate corals, stromatoporoids, brachiopods, and gastropods (e.g. Paeckelmann 1913, 1922, 1924; Wunstorf 1931; Birenheide 1990; Ellerkamp 2016; Ellerkamp et al. 2017, 2018). The faunal lists of W. Paeckelmann included *Scutellum costatum* as the only trilobite, which is a species of problematical taxonomic status (e.g. Basse et al. 2016). The trilobite bearing lithology is a middle-grey, beige to yellowish weathering limestone. Associated and more common are gastropods, ostracods, brachiopods, and crinoids.

The age of the Hofermühle South Reef has been controversial for a long time. Based on the presence of colonial rugose corals, such as *Hexagonaria segwicki* and *Phillipsastrea hennahi*, Paeckelmann (1913) assumed a Late Devonian age. However, due to the raised position of the Middle and Upper Devonian boundary, phillipsastreids are now common elements of late Givetian reefs (e.g. Errenst 1993) and elsewhere (SW England, Morocco) they enter even earlier, in the middle Givetian. In his re-evaluation of the coral fauna, which included a revision of the Paeckelmann corals, Birenheide (1990) noted both typical Middle and Late Devonian corals from the quarry, suggesting that the succession includes the transition and boundary of both. This is supported by new biostratigraphical data. Limestones from the collecting spot yielded a sparse conodont fauna (det. Z. S. Aboussalam) with *Icriodus expansus* and *Po. paradecorosus*, associated with sponge spicules, ostracods, and incrusting agglutinating foraminifers (*Tolypammina*). *Icriodus expansus* defines the shallow-water upper Givetian *I. expansus* Zone of Narkiewicz and Bultynck (2010) but the species continues into the Frasnian. *Polygnathus paradecorosus* enters in the topmost Givetian *Sk. norrisi* Zone (Aboussalam and Becker 2007) but is also common in the Frasnian. The odontopleurid site lies stratigraphically below a peculiar, anoxic black shale that severed the biostromal succession and which is regarded as the Basal Frasnes Event layer (Ellerkamp et al. 2018). A second, thinner black shale follows slightly higher. Some support comes from a conodont fauna collected from the top of the steep quarry wall,
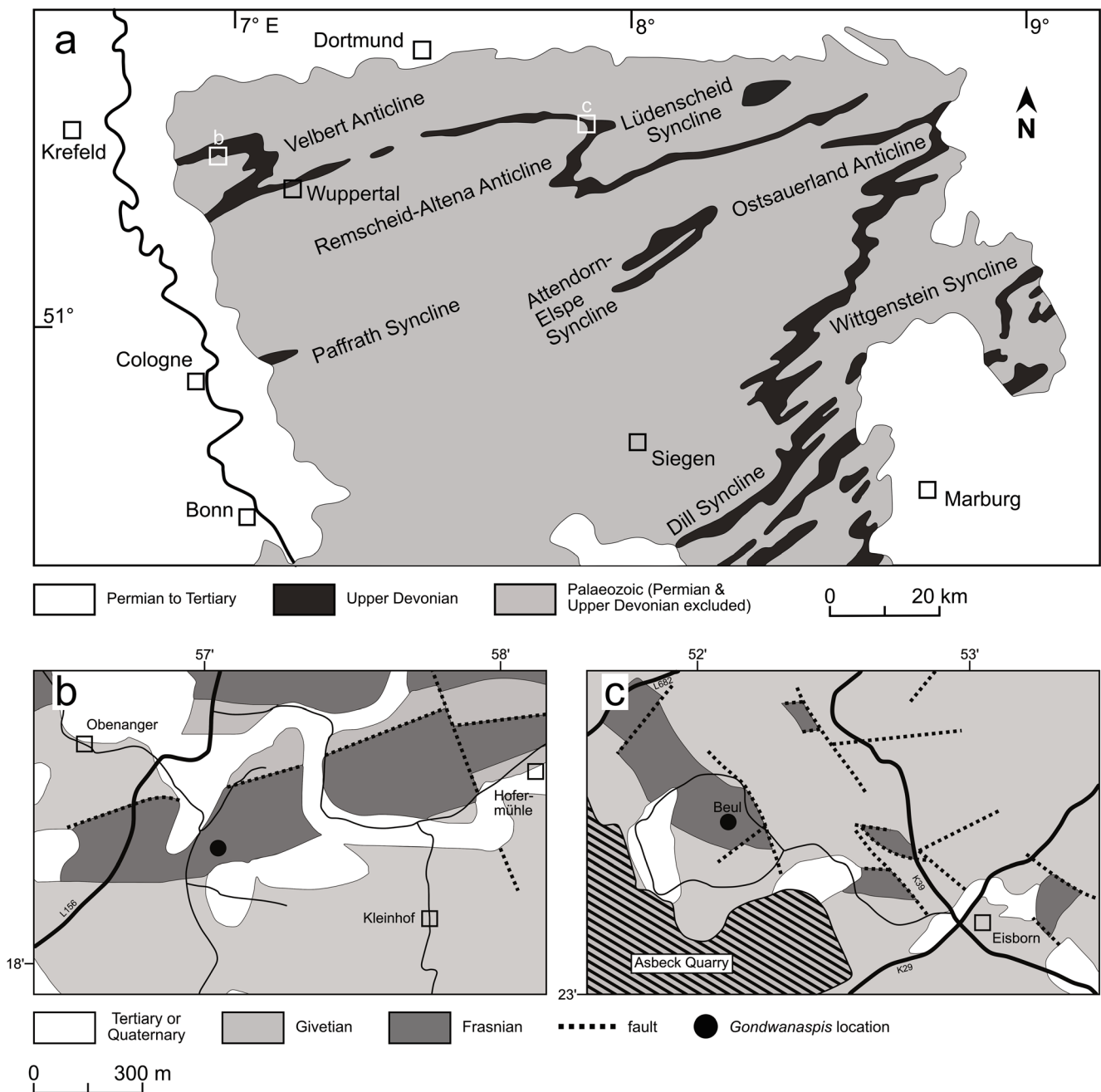
Fig. 1 a Geographic and geologic overview of the Rhenish Massif with the two *Gondwanaspis* locations (**b, c** redrawn and modified after Hartkopf-Fröder et al. 2007). **b** Geographical and geological overview of the Hofermühle South Quarry; *Gondwanaspis* location is indicated by black dot (drawn after mapsheet 4607 Kettwig and GEOportal.NRW 2020). **c** Geographical and geological overview of the Beul section; *Gondwanaspis* location is indicated by black dot (drawn after mapsheet 4613 and GEOportal.NRW 2020)

which included, apart from *Po. alatus* and *Po. webbi*, the Frasnian index species (Narkiewicz and Bultynck, 2010) *I. symmetricus*. Unfortunately, the precise relations between this sample and the main black shale are not clear. But a new record of a *Stringocephalus* (leg. M. Schürmann, Düsseldorf) confirms that the lower parts of the quarry are of (early) late Givetian age. In the absence of *I. symmetricus*, a topmost Givetian age for the odontopleurid site is likely.

Systematic Palaeontology

Figured and described specimens of this study are housed in the LWL Museum für Naturkunde Münster (WMNM). Morphological terms for trilobites are used in the sense of Whittington and Kelly (1997).

Order Odontopleurida Whittington, 1959

Family Odontopleuridae Burmeister, 1843
Subfamily Acidaspidinae Salter, 1864
Genus *Gondwanaspis* Feist, 2002

Type species: *Gondwanaspis mrirtensis* Feist, 2002
Assigned species: *G. dracula* Feist and McNamara, 2007, upper Frasnian (MN zones 11–12), Canning Basin, Australia and upper Frasnian (MN Zone 12), southeastern Rhenish Massif, Germany

G. eisbornensis n. sp., probably lower Frasnian (MN zones 1–2), northern Rhenish Massif, Germany

G. harborti (Richter, 1909), upper Frasnian (Iberg Limestone s. str.), Harz Mountains, upper Frasnian ("Iberg Limestone" of Dorp, Wuppertal-Elberfeld), northern Rhenish Massif, and upper Frasnian, (ex aff. *harborti* of Richter and Richter 1917 from Sessacker = *harbort*i Richter and Richter, 1926, UD I–J, top of interval with *Ponticeras sandbergeri*, Matern, 1931, = MN Zone 12, Becker et al. 1993), southern Rhenish Massif, all Germany

G.? sp. cf. *G.? harborti* of Basse and Müller (2004) "*Pharciceras* Beds",? lower Frasnian, northern Rhenish Massif, Germany

G. mrirtensis Feist, 2002, uppermost Frasnian (upper part of MN Zone 13a; compare Becker et al. 2020), eastern part of western Moroccan Meseta, and (cf.) Montagne Noire, southern France (see Feist and Schindler 1994, noting small differences)

G. aff. *mrirtensis* in Feist and McNamara (2007) upper Frasnian (MN Zone 12), Montagne Noire, southern France

G. prisca Feist and McNamara, 2007, upper lower Frasnian (MN Zone 4), Montagne Noire, southern France

G. schloesseri n. sp., probably topmost Givetian (*Sk. norrisi* Zone), northwestern Rhenish Massif, Germany

G. spinosa Feist and McNamara, 2007, upper Frasnian (MN zones 11–12), Canning Basin, Australia

G. tenella (Maximova, 1960), lower Frasnian, Gerikhova Limestone (= Kamenevka Formation), Gryaznukha Brook, Rudny Altai, southern Siberia, Russia (topotype of Feist and McNamara 2007 from MN Zone 2)

G. sp. A in Feist and McNamara (2007) upper Frasnian (MN Zone 11), Canning Basin, Australia

G. sp. B in Feist and McNamara (2007) uppermost Frasnian (lower part of MN Zone 13b), Canning Basin, Australia

G. sp. C in Feist and McNamara (2007) uppermost Frasnian (lower part of MN Zone 13b), Canning Basin, Australia

Diagnosis: See Feist and McNamara (2007: p. 784).
Discussion: Feist (2002) erected *Gondwanaspis* as an independent genus based on Upper Devonian material from Morocco. In contrast, Adrain (in Jell and Adrain 2003) treated *Gondwanaspis* as a junior subjective synonym of

Taemasaspis Chatterton, 1971, originally a subgenus of *Primaspis* Richter and Richter, 1917, with the youngest species, *Taemasaspis campbelli* (Chatterton, 1971) from the upper Emsian of the Waroo Limestone, New South Wales (Chatterton 1971). On the other hand, several authors treated *Taemasaspis* as a junior subjective synonym of *Dudleyaspis* Prantl and Přibyl, 1949 (Thomas 1981; Chatterton and Perry 1983; Chatterton and Wright 1986; Feist and McNamara 2007), because the only feature to distinguish between these two genera is the presence or absence of spines on the posterior cephalon border (Chatterton and Perry 1983). This procedure is initially followed here.

At first glance, the species of *Gondwanaspis* and *Dudleyaspis* are morphological very similar but in detail there are differences in the cephalic and the pygidial morphology listed by Feist and McNamara (2007: p. 785), which allow a division at generic rank and which is followed here. Nevertheless, it cannot be excluded nor can it be proven that specimens of the mentioned genera represent an evolutionary lineage, as it was already assumed by Chatterton (1971) for the genera *Primaspis* - *Taemasaspis* - *Dudleyaspis*. The absence of posterior border spines on the cephalon seems to be an exclusive feature for Devonian species (Chatterton and Wright 1986); so far it could also not be recognised on any specimen of *Gondwanaspis*. More material, in particular from Middle Devonian strata, would be helpful for further clarification, especially considering the probable range extension of the genus to the top-Givetian. As long as there are no stratigraphically or morphologically connecting forms, *Gondwanaspis* should be treated as an autonomous genus.

Feist and McNamara (2007: fig. 5p–s) pictured a cephalon from Dorp, a district of Wuppertal-Elberfeld, which they assigned to *G. harborti*. They did not state whether this is possibly the specimen from Dorp listed by Richter and Richter (1926: p. 109). But they stated that the specimen is from the reefal Dorp Limestone and from the upper Frasnian MN zones 11–12. However, Richter and Richter (1926) clearly denoted that their specimen was from the "Iberg Limestone" at Dorp, which is significantly younger and separated from the upper Givetian/lower Frasnian true Dorp Limestone by an interval of un-named shales and turbiditic Flinz limestones with *Beloceras* (Paeckelmann 1928: p. 33), the index species of UD I–H at the top of the middle Frasnian (Becker et al. 1993). Therefore, the given late Frasnian age is justified, but not a specific position within the long substage. The Dorp specimen is morphologically very similar to the holotype of *G. harborti*, re-figured by Feist and McNamara (2007: fig. 5m, q–r), except for the slightly higher vaulted cephalon of the Dorp specimen.

Basse and Müller (2004: pl. 51, fig. 662) figured an incomplete cephalon from the construction site of the Eskeshof Hotel in Wuppertal-Elberfeld, which they

assigned with reservation to *G. harborti*. It comes from the local "*Pharciceras* Beds", interpreted as early Frasnian. However, the age of this unit is not well constrained. Flattened goniatites, collected by Paeckelmann ([1928]) as supposed pharciceratids, would indicate a late Givetian age, but the identification is too unreliable to exclude the early Frasnian. The Eskeshof Hotel and the Dorp sites are in the same geographic area but the specimen figured by Basse and Müller ([2004]) clearly differs morphologically from *G. harborti*. Therefore, Feist and McNamara ([2007]: p. 793) did not regard this specimen as conspecific with *G. harborti*, which is followed here.

Basse and Müller ([2016]: p. 16) mentioned *Gondwanaspis* from the Upper Devonian of the Lahn Syncline without further information.

Gondwanaspis schloesseri n. sp.
(Fig. 2a–h; Fig. 3a–f)

Etymology: Named after Manfred Schlösser, who collected the material among other outstanding fossils from the Hofermühle South Quarry.
Holotype: Cephalon P80971 WMNM, Fig. 2a–e.
Paratype: Pygidium P80973 WMNM, Fig. 2f–h.
Locus typicus: Hofermühle South Quarry, Heiligenhaus region, northern Velbert Anticline, northwestern Rhenish Massif, Germany.
Stratum typicum: Middle-grey biostromal limestones in the lower (southwestern) part of the Hofermühle Formation, probably top-Givetian *Sk. norrisi* Zone, locally with *Po. paradecorosus*.
**Material**: Holotype, paratype, one incomplete cephalon (positive and negative, P80972a+b WMNM), two incomplete cephalon negatives (P80970 WMNM, P80979 WMNM), five isolated, incomplete cephalon borders (P80974–P80976 WMNM, P80978a+b WMNM, P80980 WMNM), one incomplete thoracic segment axis with left pleura (P80977 WMNM).
Diagnosis: Eye ridges converging with an angle of 120°. L1 and L2 clearly separated from each other and developed as individual lobes. Frontal part of glabella, L1 and L2, and eye ridges with dense ornamentation of coarse tubercles. Other parts of cephalon with less pronounced ornamentation of secondary tubercles. Genal spines straight in the first third, then bent by nearly 90°. Pygidium wide, with slightly adaxially curving major and secondary border spines.
Description of Cephalon: Maximum transversal cephalon width, without genal spines, 2.2 times the sagittal cephalon length. Moderate to gently convexity in frontal view (Fig. 2c). L2 clearly differentiated from the glabella. In contrast, L1 with a somewhat smoother transition to adjacent areas. L2 in dorsal view rounded to oval in outline. L1 rounded to globular, approximately twice as big as L2. Lateral glabellar lobes clearly

separated from each other. L3 absent or developed as small hump, indistinctly separated from abaxial part of the median glabellar lobe, but clearly differentiated from L2 (Fig. 2a). Sagittal length of median glabellar lobe nearly 1.9 times of maximum transversal width. Maximum transversal width of cephalon without spines about 6.1 times of maximum transversal width of median glabellar lobe. Length of glabella is approximately 1.8 times of maximum width of median glabellar lobe. Sagittal cephalon length is 1.5 times the sagittal length of median glabellar lobe. Median glabellar lobe separated from lateral glabellar lobes by furrows diverging slightly in sagittal direction. In the area of the posterior edge of L2, adaxially curving, ending at the transition from the eye ridges to the glabella (Fig. 2a). In frontal view, height of L1 and L2 clearly lower than the maximum height of the median glabellar lobe. Maximum height of L2 clearly lower than maximum height of L1 (Fig. 2c). In lateral view, maximum height of the median glabellar lobe lying approximately on the transversal line of the anterior edge of L1. Height of median glabellar lobe slightly lower than height of occipital ring in lateral view (Fig. 2d). Outline of median glabellar lobe evenly curved and slightly rising towards the posterior end in lateral view. Anterior part first slightly curving down, steepening towards the preglabellar furrow (Fig. 2d). Only at the abaxial areas of the median glabellar lobe clearly established (Fig. 2a). In its adaxial course, shallower and medially not detectable (Fig. 2d). Frontal glabellar lobe in dorsal view rounded. Therefore, preglabellar field medially narrow (sagittal) and abaxially slightly widening (exsagittal, Fig. 2a). Abaxial part of median glabellar lobe anterior to L2 descending into a shallower triangular area and merging with eye ridges at the midlevel of L2 (Fig. 2a). When developed at all, L3 lies within this triangle shaped area (Fig. 3b). Anterior cephalon border in front of the median glabellar lobe slightly inflated in frontal view (Fig. 2c) and slightly set back posteriorly in the area of the exsagittal tangents of adaxial edges of L2 (Fig. 2a). In dorsal view, this part of the anterior border is only slightly curved. Spines are only developed at the adaxial edges. In frontal view, recessed part of the cephalon border curving ventrally and less inflated than the neighbouring parts of the cephalon border (Fig. 2c). Sagittal length of median glabellar lobe 2.8 times of sagittal length of occipital ring. The latter trapezoidal in dorsal view (Figs. 2a, 3a). Transversal length of posterior part slightly higher then length of anterior part. Occipital organ developed as circular elevation in the sagittal middle of the occipital ring (Figs. 2a, d, 3a, d). Lateral occipital lobes drop-shaped, slightly inflated in lateral view, and completely separated against occipital ring (Fig. 2a, d). Eyes oval-shaped in dorsal view (Figs. 2a, 3a). Anterior edge at the level of anterior edge of L1 (Fig. 2a). In lateral view, highly elevated (Fig. 3c). Maximum height corresponding to height of L2 (Fig. 2c). In dorsal view, midpoint of eyes somewhat shifted posteriorly from the mid-point of the exsagittal
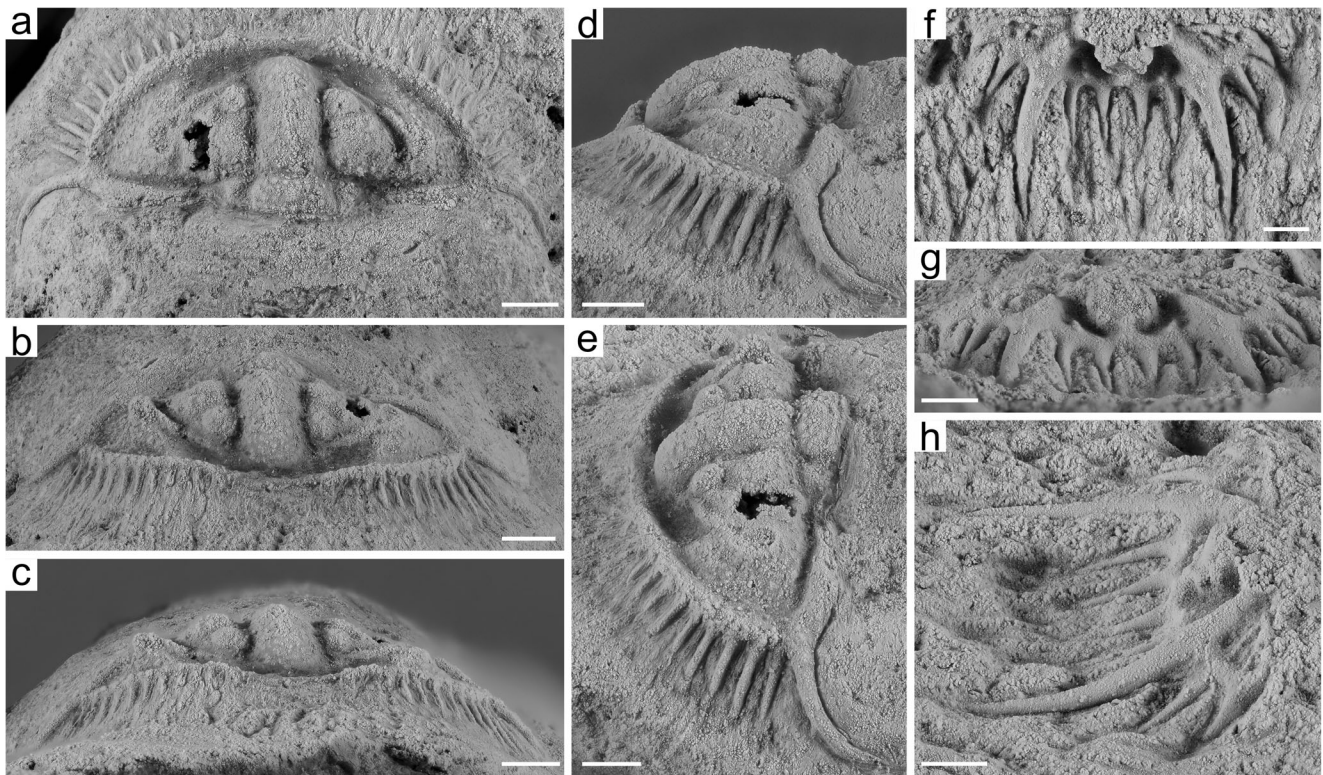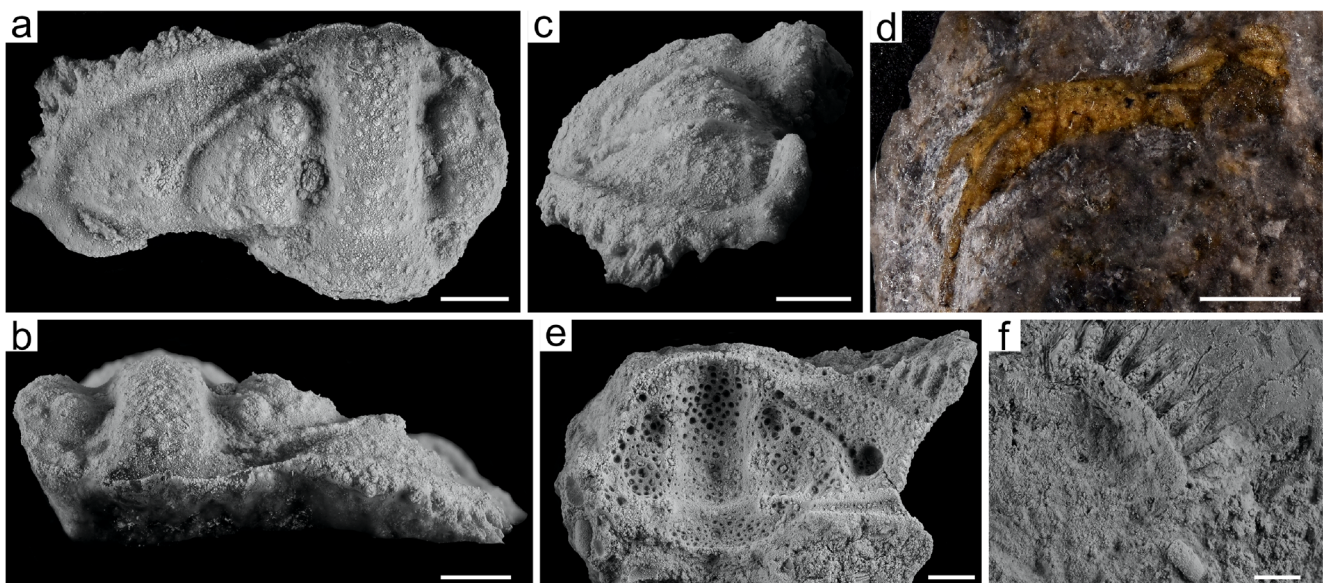
Fig. 2 *Gondwanaspis schloesseri* n. sp. from the Hofermühle South Quarry, probably top-Givetian, Velbert Anticline. **a–e** holotype, cephalon P80971 WMNM, in **a** dorsal, **b** frontal oblique, **c** frontal, **d** lateral, and **e** lateral oblique views. **f–h** paratype, pygidium P80973 WMNM, in **f** dorsal, **g** oblique frontal, and **h** frontal views. Scale bar equals 1 mm

connecting line between the anterior and posterior furrow (Figs. 2a, 3a). Eye ridges nearly straight, narrowing slightly anteriorly, in the area of the eye lobe highly raised up, and shallowing anteriorly, converging with an angle of 120°, at the base of the eye bending towards sagittal line (Figs. 2a, c, 3a–b). Adaxial part of posterior fixigena vaulted under the maximum height of L1 and L2, sloping with an angle of approximately 45° to the eye lobes (Figs. 2c–d, 3b–c). Posterior part

Fig. 3 *Gondwanaspis schloesseri* n. sp. from the Hofermühle South Quarry, probably top-Givetian, Velbert Anticline. **a–c** cephalon P80972a WMNM, in **a** dorsal, **b** frontal, and **c** lateral views. **d** thoracic segment P80977 WMNM in dorsal view. **e** cephalon P80972b WMNM in dorsal view. **f** isolated cephalon border P80976 WMNM in dorsal view. Scale bar equals 1 mm

sloping with approximately 80° to posterior border, adaxially separated from occipital lobes by a distinct furrow, abaxially less clearly developed, and merging with lateral occipital lobes (Figs. 2a, d, 3c). Posterior border adaxially narrow, widening abaxially, slightly to medium vaulted in lateral view (Fig. 2d). Highest bulge at the level of the outer edge of the eye lobe, flattening abaxially from this point, turning at about 25° in the last third of the transverse course in dorsal view (Fig. 2d). Posterior border furrow in the area of the occipital lobe shallow but detectable; abaxially deeper, flattening again from the area of the abaxial edge of the eye lobe (Fig. 2a, e). Lateral border in area of genal spines sloping anteriorly with an angle of approximately 60° in lateral view, not vaulted (Fig. 2d). Width of lateral border constant. Anterolateral border furrows in the area of the genal angle not recognisable. Anterior to genal angle, very shallow and at the level of adaxial edge of eye lobe not recognisable (Fig. 2a, e). Genal spines in the first third straight, pointed posteriorly with an angle of approximately 20° from the transversal direction, then more strongly curved backwards (Fig. 2a, e). In frontal view, dipping with an angle of 45–50° under the cephalon, widest in the area of the genal angle narrowing slightly to their posterior end (Fig. 2c-e). In lateral view, nearly circular (Fig. 2d). 12 spines on each side of the cephalon, genal spines excluded (Fig. 2a–b). Anterior spines steeper than posterior ones (Fig. 2c). Spines straight, circular, and narrowing only slightly to the tip, not perpendicular to the cephalon, but somewhat more inclined to the sagittal direction (Fig. 2a, c–d). Length of spines decreasing to the anterior part of the cephalon border. Distance between most anterior spine and adaxially following spine approximately twice as large as between the other border spines (Fig. 2a, c). Base of most posterior spine merging with base of genal spine (Fig. 2d–e). Sculpture of coarse tubercles in different sizes closely packed over the whole cephalon (Figs. 2a, 3a, e). Granulation only in small areas, such as the anterior L3, parts of the cephalon border, or rarely between larger tubercles. Coarsest tuberculation on anterior part of median glabellar lobe, L1, and L2 (Fig. 3e).

Thorax: Axis and pleural ridges moderately vaulted. Anterior spine short, abaxially, beyond fulcrum, straight, only slightly bending backwards (Fig. 3d). Posterior spine long, first half, abaxially beyond fulcrum, straight, bending backwards with an angle of approximately 20°, then curving stronger posteriorly (Fig. 3d). First half only slightly narrowing, then tapering somewhat stronger towards posterior end. Posterior spine with prominent, granulated lobe at the area of fulcrum (Fig. 3d). Anterior and posterior spine with very fine granulation, especially abaxially of fulcrum (Fig. 3d).

Pygidium: Transversal width 3.5 times of sagittal length without spines. Rhachis arched nearly semicircular, elevated well above all other parts in rear view (Fig. 2f–g). Posterior part of axial furrow developed as deep depression, less well-defined anteriorly, but still recognisable (Fig. 2f). Two well-defined axial rings with abaxially deeply incised furrows and a questionable terminal piece (Fig. 2f, h). Narrow median ridge connecting posterior part with posterior border (Fig. 2g–h). Transversal width of first axial ring is 1.8 time the transversal width of second axial ring. First three pleural ridges well-defined, slightly curving backwards or nearly straight, extending into border spines (Fig. 2d, h). Remaining two pleural ridges ill-defined. Posterior and lateral border wide and slightly vaulted (Fig. 2f–g). Border furrow ill-defined but recognisable. In rear view, posterior border between major spines curving down (Fig. 2g). Pygidium border with one pair of major border spines and four pairs of secondary border spines (Fig. 2f). Length of major border spines is two times the sagittal length of pygidium without spines. Major border spines slightly curved towards the sagittal direction and stronger bending downwards, slightly narrowing to posterior end (Fig. 2f). In rear view, nearly semicircular vaulted (Fig. 2g). Secondary border spines between major spines of equal length, approximately half the length of major spines (Fig. 2f). Only slightly curved or nearly straight. Inner pair somewhat broader at junction with the border than outer pair of spines (Fig. 2f–g). Outer pair slightly stronger vaulted in rear view than inner pair, curving ventrally with the same angle as major border spines (Fig. 2g). Sculpture consists of sparse, inconspicuous tuberculation on the border and the base of the major border spines, less common on the secondary border spines. Wide-spaced granulation is developed on all parts of the pygidium (Fig. 2f–h).

Discussion: *Gondwanaspis schloesseri* n. sp. is the so far oldest known representative of the genus, extending the range of the genus probably to the top-Middle Devonian. In addition, it is one of the few species, where the pygidium is known. This allows a detailed morphological differentiation against members of the *Primaspis - Taemasaspis - Dudleyaspis* species complex from Lower Devonian or older strata, which cannot always be done without doubts based only on cephalic features (Basse and Müller 2004). As already mentioned by Feist and McNamara (2007), the pygidium of *Gondwanaspis* is wider (transversally) than the pygidium of *Dudleyaspis*. The length to width ratio is 3.5 in *G. schloesseri* n. sp. Chatterton (1971: pl. 11, fig. 24) figured a pygidium of *Dudleyaspis campbelli* which is comparable in size with the pygidium of *G. schloesseri* n. sp., and the youngest known species of *Dudleyaspis* from upper Emsian strata of New South Wales. The length to width ratio of this specimen is 2.7. Other pygidia figured by this author are significantly smaller, but show similar ratios. All other published pygidia of *Gondwanaspis* show similar ratios as *G. schloesseri* n. sp., ranging from 3.2–3.7. Furthermore, Chatterton (1971: pl. 11, figs. 19–20) figured a pygidium of *D. campbelli*, where a third pair of secondary outer border spines is indicated by small extensions at the abaxial edge of the pygidium. A feature

which is so far only known from *G. spinosa*. In addition, the curving down border between the two major border spines may be an exclusive feature for *Gondwanaspis*. However, this has to be further proven because it cannot be verified in the previously published material from *Gondwanaspis*, nor in the material of *Dudleyaspis*.

Gondwanaspis schloesseri n. sp. is morphologically and stratigraphically close to *G. eisbornensis* n. sp.; both derive from biostromal facies. *Gondwanaspis eisbornensis* n. sp. differs in having a wider cephalon in relation to its length, a more strongly curved abaxial posterior cephalon border, stronger backwards arching genal spines, a higher overall vaulting in frontal view, and a somewhat lesser convergence angle of the eye ridges. The cephalon of *G. eisbornensis* n. sp. is over three times bigger than that of *G. schloesseri* n. sp. But, nevertheless, the morphological differences justify a separation at species level. In addition, in comparison with previous *Gondwanaspis* records, adult size is probably a meaningful species character.

Among Rhenish representatives, *G. dracula* from the upper Frasnian of Sessacker is morphologically close to *G. schloesseri* n. sp. but differs in less curved major genal spines, a somewhat narrower transversal glabella, and less pronounced L1 and L2.

The holotype of *G. harborti* from the Iberg Limestone of the Harz Mountains was re-figured by Feist and McNamara (2007: figs. 5m, q–r). It differs from the new species by a less vaulted glabella in frontal view, more pronounced eye ridges, and a clearly developed L3. The Dorp specimen of *G. harborti*, figured by Feist and McNamara (2007: fig. 5p, s), is closer to *G. schloesseri* n. sp. Although the vaulting of the cephalon in frontal view as well as the curving of the major genal spines in dorsal view are quite similar to that of *G. schloesseri* n. sp., it clearly differs in a stronger anterior tapering of the glabella. Furthermore, L1 and L2 are well demarcated against each other in *G. harborti*, while this feature is rather indistinct in *G. schloesseri* n. sp. In addition, the convergence angle of the eye ridges in *G. schloesseri* n. sp. is slightly lower than in *G. harborti* and the tuberculation of *G. schloesseri* n. sp. is densely packed with partly coarser elements.

The previously oldest known species of the genus are *G. prisca* from the Montagne Noire and *G. tenella* from the Rudny Altai. Both are early Frasnian in age. *Gondwanaspis prisca* clearly differs in a more rectangular anterior outline of the glabella. It is one of the few other species, where the pygidium is known (Feist and McNamara 2007: fig. 5o). In relation to its length, it is comparatively narrow in comparison to *G. schloesseri* n. sp. and the major and secondary border spines are more straight rather than curved.

Gondwanaspis tenella differs from *G. schloesseri* n. sp. also by a more rectangular anterior glabella as well as by narrow L1 and L2. The ratio of cephalon width to length is somewhat higher than in *G. schloesseri* n. sp. and the major genal spines are less curving backwards.

The cephalon of the youngest known representative of the genus, *G. mrirtensis*, is only slightly vaulted in frontal view, and the adaxial part of the major genal spines are facing forward. L1 and L2 are less clearly developed, and the sculpture consists mainly of fine granulation, with only a few coarse tubercles.

The ratio of pygidium width to length in *G. spinosa* is comparable to that of *G. schloesseri* n. sp. The border spines of the latter are stronger curved, especially the major border spines. The vaulting of the cephalon in frontal view is less high in *G. spinosa*. The major cephalic border spines are adaxially straight and the convergence angle of the eye ridges is higher in *G. spinosa*. The sculpture of *G. spinosa* consists of a few, widely-spaced, coarse tubercles.

There are three species of *Gondwanaspis* in open nomenclature, all from the upper Frasnian Virgin Hill Formation of the Canning Basin, Western Australia. *Gondwanaspis* sp. A differs from *G. schloesseri* n. sp. in a denser tuberculation of the cephalon and less developed L1 and L2. The eye lobe of *Gondwanaspis* sp. B is positioned more anteriorly and bigger. The latter is also true for *Gondwanaspis* sp. C. The genal spines of this species are also less curved, running straight until the middle, then bending only slightly backwards.

Gondwanaspis eisbornensis n. sp.
(Fig. 4a-h)

Etymology: Named after the small village Eisborn east to the locus typicus.
Holotype: Cephalon P80981a+b WMNM, Fig. 4a–h.
Locus typicus: Beul section near Eisborn, Hönne Valley region, northern Rhenish Massif, Germany.
Stratum typicum: Eisborn Member of Hagen-Balve Formation, most likely early Frasnian but a top-Givetian age cannot be completely excluded.
**Material**: Holotype and internal silicone cast.
Diagnosis: Frontal border set back posteriorly. Genal spines strongly bent posteriorly, not merging with the posterior most border spine. Adaxial posterior fixigena highly vaulted. Eye ridges slightly curved, with a convergence angle of 115°. Eye lobes large. Frontal glabellar lobe rounded.
Description: Maximum transversal cephalon width, without genal spines, 2.4 times the sagittal cephalon length. Moderate convexity in frontal view (Fig. 4c). Glabellar lobes clearly differentiated from the glabella (Fig. 4a, g). L2 rounded to dropshaped, a little more individualized than L1 (Fig. 4a, f–g). The latter larger than L2 and somewhat oval in shape (Fig. 4a, f–g). L1 and L2 clearly separated from each other (Fig. 4a, f–g). L3 not developed. Sagittal length of median glabellar lobe nearly 1.8 times of maximum transversal width. Maximum transversal width of cephalon without spines about 7 times the maximum transversal width of median glabellar lobe. Length of median glabellar lobe approximately 1.4 times of maximum width of

median glabellar lobe. Sagittal cephalon length is approximately 1.5 times the sagittal length of median glabellar lobe. Separated from lateral glabellar lobes, straight furrows run roughly parallel to the sagittal line, anterior to L2 as deeper impressions, relatively shallower in the area of L1. At the level of the occipital lobe, they turn slightly abaxially from the parallel sagittal line and disappear in the posterior second half of the occipital lobe (Fig. 4g). In frontal view, maximum height of L1 and L2 clearly lower than the maximum height of the median glabellar lobe (Fig. 4c). Height of L2 only marginally below height of L1 (Fig. 4c). In lateral view, maximum height of the median glabellar lobe lies approximately in the transversal line of the anterior part of L1 (Fig. 4d). Height of median glabellar lobe slightly higher than maximum height of occipital lobe in lateral view (Fig. 4d). In the latter, outline of median glabellar lobe slightly rising in the posterior part to maximum glabellar height, with anterior part first slightly curving down, then curving stronger and descending steeper (Fig. 4d). Preglabellar furrow abaxially deeply incised; adaxially somewhat shallower and narrowing but always clearly developed.

Preglabellar furrow slightly bent parallel to the frontal margin of the median glabellar lobe (Fig. 4a). Lateral part of glabella anterior L2 abaxially flattening. In this area, merging with the eye ridge at the mid-level of L2 (Fig. 4a, f–h). Anterior cephalon border in front of the median glabellar lobe slightly inflated in frontal view (Fig. 4b–c). Anterior border in front of the median glabellar lobe slightly set back posteriorly in the area of the exsagittal tangents running through the mid-point of L2 (Fig. 4a, g). In dorsal view, this area is slightly curved (Fig. 4a). Spines are only developed at the adaxial edges (Fig. 4a). Axial furrow in the anterior part shallow and narrow, nearly not visible. Posterior part, starting from the posterior half of L2, slightly deeper incised and widening towards posterior part of cephalon (Fig. 4a–b, e, g). Length of median glabellar lobe approximately 2.4 times of sagittal length of occipital ring. Only slightly curved sagittally/exsagittally in lateral view (Fig. 4d). Lateral occipital lobes weakly separated and not inflated (Fig. 4a, d). Eyes in dorsal view spherical, with midpoint barely at the centre of the exsagittal connecting line between the anterior and posterior furrow; rather shifted slightly towards the
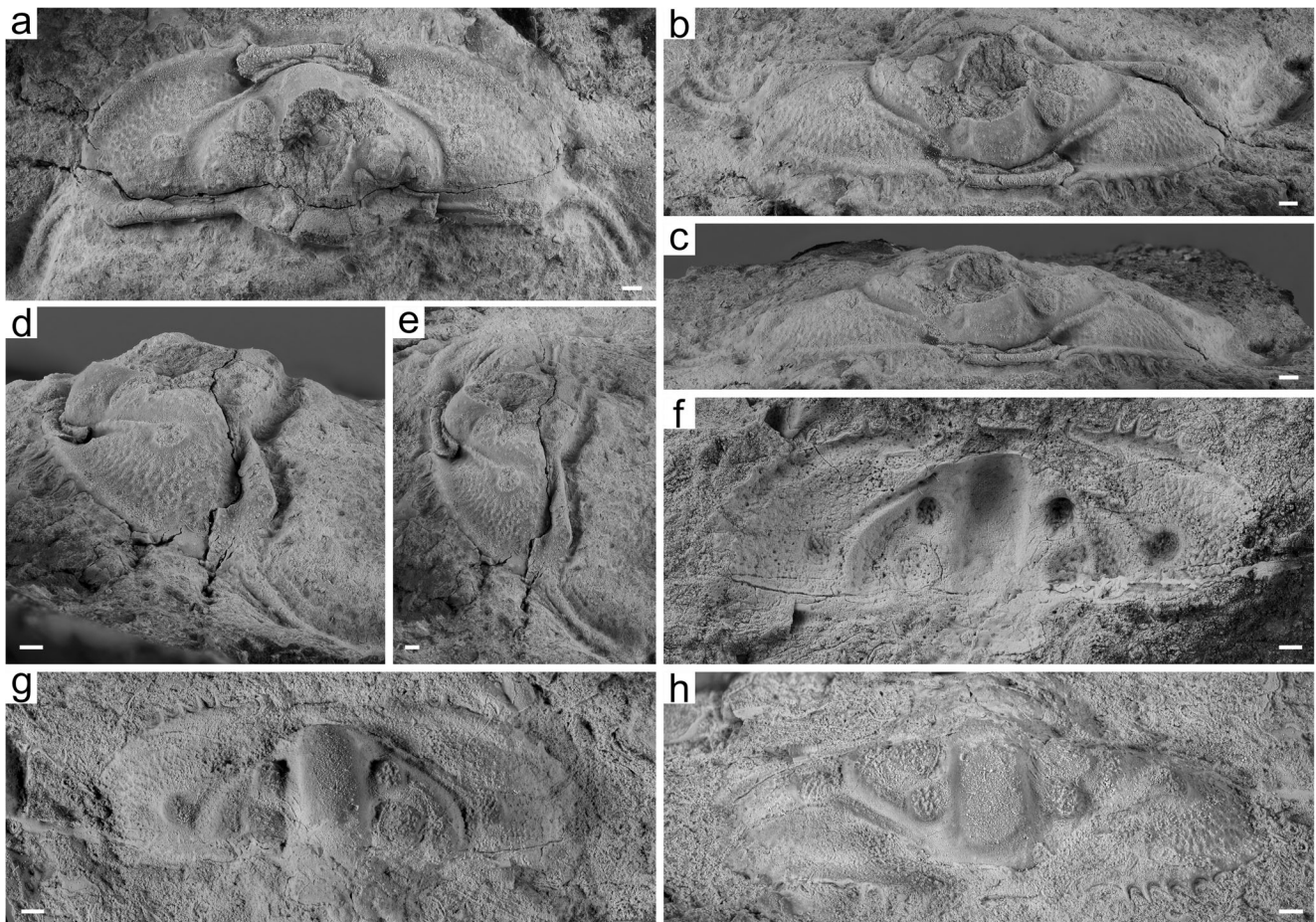
Fig. 4 *Gondwanaspis eisbornensis* n. sp. from Beul near Eisborn, probably basal Frasnian, Hönne Valley region, northern Sauerland. **a–e** holotype, cephalon P80981a WMNM, in **a** dorsal, **b** oblique frontal, **c** frontal, **d** lateral, and **e** oblique dorsal views. **f** holotype, internal cast of cephalon P80981b WMNM in dorsal view. **g–h** holotype, silicone cast of cephalon P80981b WMNM in **g** dorsal and **h** oblique frontal views. Scale bar equals 1 mm

posterior part (Fig. 4a, g). Anterior edge on the level of the posterior edge of L2 (Fig. 4a, g). Eye ridges in dorsal view with a very low convexity (Fig. 4a, g). Width from the eye lobes to anterior border of L2 nearly constant, then thinning anteriorly (Fig. 4a, g). Angle of convergence at about 115°. Adaxial part of posterior fixigena vaulted slightly under the maximum height of L1 and L2, steeply sloping to the abaxial posterior part of fixigena and to the occipital lobes, merging with these (Fig. 4d). Internal cast of librigenal, especially in the marginal area, with meshwork of anastomosing ridges (Fig. 4f). Posterior border at the exsagittal level of adaxial edge of L1 merging with posterior border furrow, abaxially at the exsagittal level of the eye highly arched and oval in cross section, flattening abaxially of this point, merging with the border furrow clearly before it reaches the genal angle, and turning at about 40° in the last quarter of the transverse course in dorsal view (Fig. 4a). Lateral border in area of genal spines sloping anteriorly with an angle of approximately 70° in lateral view, not vaulted (Fig. 4d). Maximum width of lateral border anterior genal spines (Fig. 4e). Only slightly narrowing anteriorly to the frontal border. Anterolateral border furrows in the area of the genal angle not recognisable, anterior to genal angle very shallow, and at the level of abaxial edge of L1 not recognisable (Fig. 4a). Genal spines directly curved posteriorly and downwards at the transition to the genal angles (Fig. 4a, d). Lateral to anterior border wide, slightly arched at the most anterior edge. With at least seven spines per side, genal spines excluded, widest at their base and narrowing anteriorly (Fig. 4a, d). Spines considerably curved downward and turning slightly against the direction of the cephalon border, dipping with 70–80° from the horizontal and, thereby, steeper than the genal spines (Fig. 4d). Distance between most anterior spine and adaxial following spine approximately twice as large as between the other border spines (Fig. 4a). Sculpture only partly preserved, consisting of coarse tubercle, pearl cord-like oriented on the eye ridges (Fig. 4b). Space between tubercles approximately 1.5–2 times tubercle diameter. Frontal border anterior of frontal glabellar lobe with closely packed granulation different in size and partially merging (Figs. 4a, f). L1 and L2 with coarse, closely packed tuberculation, comparatively larger then tuberculation of eye ridges (Fig. 4f, h). Posterior border with shallow wide-spaced tuberculation (Fig. 4a, f). Genal spines with granulation comparable to frontal border (Fig. 4a, g). In the range of the genal angle with suppressed tuberculation (Fig. 4a, g).

Discussion: *Gondwanaspis dracula* and *G. harborti* were so far the only named species of *Gondwanaspis* from Germany. Both are late Frasnian in age. *Gondwanaspis dracula* is known from an incomplete cephalon from the Sessacker near Oberscheld in the southern Rhenish Massif (Richter and Richter 1926; Matern 1927, 1931). It was re-figured by Feist and McNamara (2007: fig. 4r). It is slightly smaller than the material presented here but has the same ratio of cephalon width to length (0.42) while the holotype of *G. dracula*,

figured by Feist and McNamara (Feist and McNamara 2007: fig. 4j), from the upper Frasnian of the Virgin Hills Formation, Canning Basin, has a slightly smaller ratio of 0.38. *Gondwanaspis eisbornensis* n. sp. differs from *G. dracula* by its inflated glabellar lobes, slightly arched eye ridges, and genal spines that are clearly bent backwards.

The holotype of *G. harborti* from the Iberg Limestone of the Harz Mountains was re-figured by Feist and McNamara (2007: fig. 5m, q–r). It differs from the new Beul species in having more pronounced L1 and L2; L3 is also clearly visible. The eye ridges are straight, with an angle of 129° to the sagittal line. The posterior part of the fixigena is less swollen and the median glabellar lobe is relatively narrower in terms of the length of the median glabellar lobe. This is also true for the specimen of *G. harborti* from Dorp figured by Feist and McNamara (2007: fig. 5p–s), although the general vaulting of the cephalon is comparable to *G. eisbornensis* n. sp. In comparison to the holotype, the median glabellar lobe seems to be wider in relation to the length, and the preglabellar field is less clearly developed. The angle of the eye ridges is, with 134° to the sagittal line, somewhat higher than in the holotype of *G. harborti*. Furthermore, the genal spines of that species are fused at their bases with the most posterior spine of the librigenal border, which is not the case in the Beul species.

Gondwanaspis prisca shares some morphological features with the slightly older *G. eisbornensis* n. sp., the development of L1-L2, the vaulting of the glabella lobe area, and the position of the genal spines on the margin. It clearly differs in having a more rectangular median glabellar lobe with a prominent straight anterior border, more clearly defined eye ridges, and genal spines, which are straight at the attachment point to the cephalic border.

The holotype of *G. tenella* was figured by Maximova (1960: pl. 8, fig. 14). In some features, e.g. in the outline of the central glabellar lobe and in the definition L1-L2, it seems to be morphological similar to *G. prisca*, which can be distinguished by more posteriorly positioned eyes. Feist and McNamara (2007: fig. 5i) figured a new, incomplete cephalon, which they assigned to *G. tenella*. It can be seen, that the angle of its eye ridge is less steep and the genal spines are less bent backwards.

Gondwanaspis mrirtensis is the youngest named species of the genus. It differs from the Beul specimen by a lower vaulting of the cephalon, in general, and the glabellar lobe area, specifically. Furthermore, the genal spines are pointed forward, a feature, which can also be observed in the somewhat older (MN Zone 11) *Gondwanaspis* sp. A of Feist and McNamara (2007) from the Canning Basin, Australia, and, less clearly, in *Gondwanaspis* sp. B of Feist and McNamara (2007), also from the Virgin Hill Formation (MN Zone 13b) of the Canning Basin. In *Gondwanaspis* sp. C of Feist and McNamara (2007), the third Canning Basin species described in open nomenclature from the Virgin Hill Formation (MN

Zone 13b), the comparatively large eyes, in relation to the cephalon length (sag.), and the ornamentation, consisting of coarse tuberculation, distinguish it from *G. eisbornensis* n. sp.

Gondwanaspis spinosa from the Canning Basin was contemporaneous with *G. harborti*. The general outline of the glabella and the shape of L1 and L2 are connecting morphological features of both species, while the angle of the eye ridges and the curvature of genal spines are separating them. The latter feature connects *G. harborti* with *G. eisbornensis* n. sp., while the genal spines of *G. spinosa* are almost straight.

Conclusions

Gondwanaspis schloesseri n. sp. and *G. eisbornensis* n. sp. extend the distribution of the genus in the probable top-Givetian and basal Frasnian of the Rhenish Massif. The two new species are close in geographical, stratigraphical, and facies distribution but can be clearly separated morphologically. Both are morphologically closer to geographically related (Rhenish) representatives than to early Frasnian species of distant regions. This leads to the assumption, that *Gondwanaspis* was a cosmopolitan genus with restricted exchange between individual populations. So far, *G. dracula* is the only species with a documented distribution in widely different basins.

Morphological relationships with Early Devonian and older species of the *Primaspis - Taemasaspis - Dudleyaspis* complex do exist but are not sufficient, especially due to the pygidial morphology, to express this at generic level. More material, especially from Lower and Middle Devonian strata, will be needed to determine their phylogeny.

Data availability All data generated or analysed during the current study are included in this published article. The trilobite originals are stored in the LWL Museum für Naturkunde Münster, Sentruper Straße 285, 48161 Münster, Germany.

Declarations

Conflict of interest The authors declare that they have no conflict of interest.

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